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ORIGINAL ARTICLE

Miocene hominoid biogeography: pulses of dispersal and differentiation

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ABSTRACT

Aim To test the hypothesis that the ancestor of the hominines (African apes and humans) had an African origin by comparing the historical biogeographical patterns of hominoids with those of two other large land mammal clades, namely the hyaenids and proboscideans.

Location Global, primarily the Old World over the last 25 Myr (Miocene to present).

Methods Creation of a general area cladogram using PACT, a new method for generating area cladograms, and interpretation of general and clade-specific speciation events involving hominoids, proboscideans and hyaenids.

Results The analysis of the areas using PACT reveals both general patterns and clade-specific exceptions to these patterns. All three groups share a general episode of species formation in Africa in the early Miocene, followed by 'out of Africa' expansion into Europe, Asia and North America, and a second general episode of species formation in Asia in the mid-Miocene, followed by 'out of Asia' expansion into Africa, Europe and North America. Finally, there were two additional 'out of Africa' events during the late Miocene and into the Pliocene, the last one setting the stage for the emergence and spread of *Homo*. In addition to these shared episodes of vicariance and dispersal, each group exhibits clade-specific within-area and peripatric speciation events.

Main conclusions The complex history of dispersal and speciation over large areas exhibited by hominoids is part of a more general history of biotic diversification by taxon pulses. Refining this scenario will require the integration of additional clades from the same areas and times, as well as more detailed palaeoclimatological, palaeoenvironmental and geological evidence.

Keywords

Biotic expansion, hominoid evolution, Hyaenidae, 'out of Africa', PACT, Proboscidea, phylogeny, taxon pulse, vicariance.

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INTRODUCTION

Few central themes in evolutionary biology generate as much interest as the question of human origins and diversification. Numerous theories have been proposed to explain the evolution and geographical distribution of hominoids. Following Begun (2002), we consider the Hominoidea (Gray, 1821) (hereafter hominoids) to be a clade comprising all species more closely related to *Homo* than to the cercopithecoids. The Hominidae (Gray, 1825) (hereafter hominids) is a clade comprising the most recent common ancestor of *Homo* and *Pongo* (the orangutans) and all its descendants. The Homininae (Gray, 1821) (hereafter hominines) is a clade comprising the most recent common ancestor of species more closely related to *Homo* than to *Pongo* and all its descendants (including the African apes), and the Hominini (Gray, 1825) (hominins) is a clade comprising the most recent common ancestor of species more closely related to *Homo* than to *Pan* and all their descendants.

Darwin (1859) suggested that Africa was the place of origin for humans, because our two closest living relatives (chimpanzees and gorillas) are found exclusively there. This

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hypothesis was supported by the discovery of Plio-Pleistocene australopiths in South Africa (Dart, 1925) and east Africa (Leakey, 1959). It gained further strength when early hominoids such as *Proconsul*, *Afropithecus* and *Kenyapithecus* were discovered at early and middle Miocene localities such as Rusinga Island, Fort Ternan, and Maboko (Hartwig, 2002 and references therein). Intense palaeontological activity has been aimed at identifying strata and recovering late Miocene-aged fossils, and of a number of late Miocene localities have been identified in Africa (including Qasr As Sahabi, Toros-Menalla, Middle Awash, Lothagam, Ngorora, Samburu, Lukeino, Manonga Valley, Berg Aukas, Djebel Krechem, Menacer, Aït Kandoula and Langebaanweg). In spite of this, however, few of these sites have produced more than fragmentary hominoid fossils (Begun, 2001).

The paucity of fossil species more closely related to *Homo* than to *Pongo* in Africa earlier than about 6 Ma has been an enigma for scientists, most of whom attribute it to preservational bias (Benefit & McCrossin, 1995; Cote, 2004). They suggest that the late Miocene trend towards increased aridity and the spread of C_4 plants caused a contraction in the ranges of tropical taxa such as hominoids, and that therefore hominoids would have been restricted to equatorial Africa (Benefit & McCrossin, 1995; Cerling *et al.*, 1997; Pagani *et al.*, 1999). The absence of these hominoids from the African fossil record is ostensibly a result of the lack of fossil localities in equatorial Africa, where excavation and discovery are hampered by thick rain forest. This may be problematic, if, as many have suggested, hominoids are seriously underrepresented in the African fossil record. The diversity of primate species represented by the fossil record is certainly lower than that represented by living primates. If and when new fossil taxa are discovered, the conclusions we reach in this paper will have to be re-evaluated in light of the new data.

In Eurasia the opposite situation applies: hominoids (*Griphopithecus*) appear during the middle Miocene (around 16 Ma) and diversify both morphologically and geographically (Andrews & Tobien, 1977; Heizmann & Begun, 2001). *Dryopithecus* is found in France, Spain, and Hungary; *Oreopithecus* in Italy; *Ouranopithecus* and *Graecopithecus* in Greece; and *Ankarapithecus* in Turkey (see Begun, 2002 and references therein). In Asia, *Gigantopithecus* and *Sivapithecus* evolve in India and Pakistan, and *Lufengpithecus* in China (see Kelley, 2002 and references therein). These Eurasian species appear to persist until the late Miocene, but disappear by the time hominins appear in the African fossil record.

The conventional explanation for these observations has been that the Eurasian Invasion was a short-lived side venture from the main story, the evolution of the hominines occurring in Africa. Because the living African apes and the extinct sister taxa of *Homo* (*Australopithecus*, *Ardipithecus*, *Paranthropus*, etc.) are found exclusively in Africa, most researchers have assumed that the common ancestor to these taxa was also African. Some have made the further assumption that, because the earliest hominoids are African, the lineage leading to living hominines (*Pan*, *Gorilla* and *Homo*) remained exclusively African throughout its duration (Darwin, 1859; Andrews, 1992; Benefit & McCrossin, 1995; Moyà-Solà & Köhler, 1996; Sen, 1998; Moyà-Solà *et al.*, 2004; Pilbeam & Young, 2004; Senut & Pickford, 2004). Moyà-Solà & Köhler (1996) further suggested that the late Miocene hominoid *Dryopithecus* shares functional and morphological characters for suspensory locomotion with *Sivapithecus*, and that this indicates 'phylogenetic proximity'. Benefit & McCrossin (1995) argued that none of the European Miocene hominoids share derived characters with the living ape-human clade, and that therefore they are not part of the clade. Both of these hypotheses are consistent with the African origins theory; however, neither is supported by formal phylogenetic analysis.

Recent phylogenetic analyses of hominoids have produced a more robust basis from which inferences about the evolution of humans and their closest relatives can be derived (Begun *et al.*, 1997; Strait *et al.*, 1997). Begun *et al.* (1997) analysed 247 characters and eight taxa, with an outgroup composed of a number of fossil cercopithecines and platyrrhines. This resulted in one most parsimonious tree, consistent with molecular phylogenies (Shoshani *et al.*, 1996; Goodman *et al.*, 1998). The analysis placed *Dryopithecus* as the sister taxon to the hominines. Rather than postulating a hypothetical ancestor or series of ancestors of African distribution, Begun (1997, 2000, 2001) and Stewart & Disotell (1998) suggested that the most parsimonious explanation was that the common ancestor of modern humans and the African apes was Eurasian.

A phylogeny and knowledge of the geographical distributions of taxa are not by themselves sufficient to resolve complex histories of speciation for any given group (e.g. Brooks & McLennan, 2002; Green *et al.*, 2002; Donoghue & Moore, 2003; Brooks *et al.*, 2004; Halas *et al.*, 2005). It is probable that large-scale geological or environmental phenomena have affected the evolution of the hominoid clade, so the story of hominoid evolution is likely to be more complex than previous studies have hypothesized. It is even possible that all previous hypotheses are partially true, each pointing to part of a larger story. Comparison of the historical biogeography of hominoids with that of other clades existing at the same time and in the same places, in this study the proboscideans and hyaenids, can reveal events that affected members of all clades (general events), as well as clade-specific events. In this manner, we can use a form of reciprocal illumination to help us to infer to what extent hominoid diversification was the product of general evolutionary radiations affecting other members of their biotas as well.

METHODS

The phylogenies

We chose proboscideans and hyaenids over other taxa for three reasons: first, they are large vertebrates that share broadly similar habitat preferences; second, they are frequently found at the same fossil localities, indicating that they shared a biogeographical distribution in the past; and finally, because there were phylogenies including extinct species available in the literature. The choice of input phylogenies is clearly the most important and also the most controversial decision made in a historical biogeographical analysis such as this. There is rarely a consensus in the literature amongst specialists on a given clade as to which data set and tree topology best reflect the evolution of the group. Our criteria for choosing one particular topology over another were to choose the analysis that included the most data (i.e. number of characters and number of taxa), and that where possible the characters should not be restricted to one morphological set (i.e. only cranio-dental). Where there were conflicting analyses (one with more characters and one with more taxa), we chose the one with the most taxa included. The topologies of the input phylogenies do determine the inferences made regarding the historical biogeography of a clade, and where debate exists, we must be aware that there are alternative reconstructions. The inferences we make are therefore hypotheses that are testable with the addition of new data.

Shoshani (1996) and Tassy (1994, 1996) published separate analyses of the Proboscidea that resulted in similar, but not identical, trees. Shoshani included 123 characters and 39 taxa (with two outgroups) to investigate the relationships within the gomphotheres. Tassy's analysis used 138 characters and 22 taxa (with three outgroups). Tassy collapsed the 'ambelodonts', 'gomphotheres', and Mammutidae, while Shoshani ran the analysis with genera as terminal taxa. The differences between the results are: in Tassy's analysis, *Stegotetrabelodon* falls more basally; the 'amebelodontidae' and 'gomphotheres' do not form a monophyletic group; and *Anancus*, *Paratetralophodon* and *Stegotetrabelodon* form an unresolved polytomy (Tassy, 1996). A third alternative hypothesis, Kalb *et al.*'s (1996b) analysis, includes only 18 taxa and 34 cranial and dental characters. We chose Shoshani's (1996) unordered 50% majority-rule consensus tree of 600 most-parsimonious trees (MPTs) because he included more taxa (monophyletic genera) than did either of the other two (illustrated in Fig. 1). We used the crown of the tree, from *Phiomia* upwards, because the earlier taxa are outside the temporal range of the hominoid and hyaenid comparisons. Distributional and temporal data are from Shoshani & Tassy (1996) (Table 1).

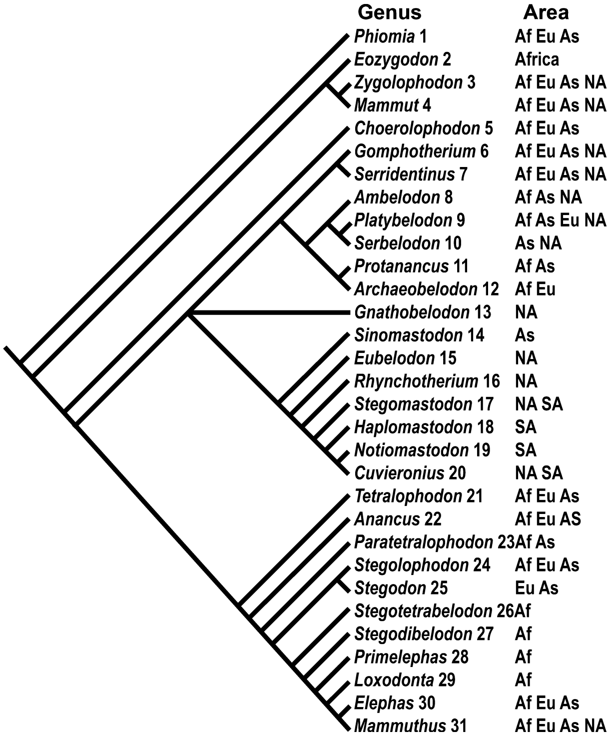

Figure 1 Proboscidean taxon and area cladogram (redrawn and modified from Shoshani, 1996). Area(s) beside the genus name indicate the geographical range(s) in which the genus is found. (Range data are from Shoshani & Tassy, 1996 and Fortelius, 2005.) AS: Asia, AF: Africa, EU: Europe, NA: North America, SA: South America.

The hyaenid phylogeny is from Werdelin & Solounias (1996), a revision of Werdelin & Solounias (1991) and Werdelin *et al.* (1994). The original included 18 genera and 20 characters (all of which are cranio-dental) and produced 16 MPTs of 51 steps with a CI of 0.53. Their (1996) revised version, which we use, included 24 genera (Fig. 2). The tree differs from that of Werdelin & Turner (1996) with respect to the placement of *Tungurictis*, *Tonxinictis* and *Thalassictis*. Werdelin & Solounias (1996) found the relationships between *Tungurictis* and *Tonxinictis* unresolved, so we use this slightly more conservative estimate. All genera used in the analysis appear monophyletic on the tree, and at a species level form unresolved polytomies. To remain consistent with the other two input phylogenies, we collapsed monophyletic clades that resolved species relationships into genera, thereby treating these monophyletic genera as terminal branches. Some temporal and distributional data are from Werdelin & Lewis (2005) (Table 1). An alternative phylogeny was presented by Wagner (1998), in which he used stratocladistic methods to find a tree that was most parsimonious with respect to both morphology and stratigraphy. One method of evaluating the biogeographical pattern is by checking for correspondence with first appearance data. Incorporating temporal data into the initial analysis, and then using the same data to evaluate the hypothesis would introduce an unacceptable amount of circularity into this analysis, so we do not use Wagner's stratocladistic tree as an input phylogeny. We do, however, evaluate our results in light of these findings.

Most molecular phylogenies of the living hominoids have converged on one result: (*Hylobates*/*Symphalangus* (*Pongo*(*Gorilla*(*Pan*,*Homo*)))) (Purvis, 1995; Shoshani *et al.*, 1996; Goodman *et al.*, 1998; Pilbeam & Young, 2004). There have been several published phylogenetic analyses using morphological characters that include known fossil taxa. The most comprehensive phylogenetic analysis is Begun *et al.*'s analysis of 247 characters and 19 taxa (Begun *et al.*, 1997; Begun, 2001). Finarelli & Clyde (2004) modified Begun's original (1997) character matrix by excluding parsimony-uninformative characters, adding five additional characters, and combining multiple characters for the same trait. Their revised analysis includes 200 characters and 18 taxa, and results in four MPTs, the strict consensus of which we use in this analysis

Table 1 List of numbered taxa with geographical distribution and first appearance dates (FADs) rounded to the nearest 0.5 Ma. Biogeographical and first appearance data are from Shoshani & Tassy (1996), Begun (2002), Kelley (2002), Fortelius (2005) and Werdelin & Lewis (2005). Area abbreviations are as follows. AF: Africa, EU: Europe, AS: Asia, NA: North America, SA: South America

No.	Genus	Area	FAD	No.	Genus	Area	FAD	No.	Genus	Area	FAD
1	*Phiomia*	AF	25	**26**	*Stegotetrabelodon*	AF	6	**51**	*Pliocrocuta*	AF EU AS	7
2	*Eozygodon*	AF	23	**27**	*Stegodibelodon*	AF	6	**52**	*Pachycrocuta*	AF EU AS	5
3	*Zygolophodon*	AF EU AS NA	17	**28**	*Primelephas*	AF	5.5	**53**	*Crocuta*	AF EU AS	3.5
4	*Mammut*	AS NA	18	**29**	*Loxodonta*	AF	3.5	**54**	*Adcrocuta*	AF EU AS	11
5	*Choerolophodon*	AF EU AS	17	**30**	*Elephas*	AF EU AS	4	**55**	*Proconsul*	AF	24
6	*Gomphotherium*	AF EU AS	16	**31**	*Mammuthus*	AF EU AS NA	12	**56**	*Griphopithecus*	EU	16.5
7	*Serridentinus*	AF AS NA	18	**32**	*Protctitherium*	AF EU AS	18	**57**	*Kenyapithecus*	AF	14
8	*Ambelodon*	AF AS NA	8	**33**	*Proteles*	AF	3	**58**	*Equatorius*	AF	16
9	*Platybelodon*	AF EU AS NA	16	**34**	*Plioviverrops*	EU	23	**59**	*Turkanapithecus*	AF	18
10	*Serbelodon*	AS NA	12	**35**	*Tungurictis*	AS	13	**60**	*Afropithecus*	AF	18
11	*Protanancus*	AF AS	12	**36**	*Tongxinictis*	AS		**61**	*Morotopithecus*	AF	21
12	*Archaeobelodon*	AF EU	16	**37**	*Thalassictis*	EU AS	20	**62**	*Hylobates*	AS	0
13	*Gnathabelodon*	NA	12	**38**	*Ictitherium*	AF EU AS	12.5	**63**	*Oreopithecus*	EU	8
14	*Sinomastodon*	AS	10	**39**	*Hyaenotherium*	AS	11	**64**	*Dryopithecus*	EU	11.5
15	*Eubelodon*	NA	12	**40**	*Miohyaenotherium*	AS	10	**65**	*Lufengpithecus*	AS	8
16	*Rhynchotherium*	NA	8	**41**	*Hyaenictitherium*	AF EU AS	9	**66**	*Ankarapithecus*	AS	10
17	*Stegomastodon*	NA SA	4.5	**42**	*Lycyaena*	AF EU AS	9.5	**67**	*Pongo*	AS	0
18	*Haplomastodon*	SA	5	**43**	*Hyaenictis*	AF EU	11	**68**	*Sivapithecus*	AS	12.5
19	*Notiomastodon*	SA	4	**44**	*Chasmaporthetes*	AF EU AS NA	5	**69**	*Ouranopithecus*	EU	10
20	*Cuvieronius*	NA SA	5	**45**	*Palinhyaena*	AS	8	**70**	*Gorilla*	AF	0
21	*Tetralophodon*	AF EU AS	12	**46**	*Ikelohyaena*	AF	6	**71**	*Pan*	AF	0
22	*Anancus*	AF EU AS	10	**47**	*Belbus*	EU	8	**72**	*Australopithecus*	AF	4.5
23	*Paratetralophodon*	AS	10	**48**	*Leecyaena*	AF	6	**73**	*Homo*	AF EU AS NA SA	2
24	*Stegolophodon*	AS	16	**49**	*Parahyaena*	AF	2.5				
25	*Stegodon*	AF AS	8	**50**	*Hyaena*	AF AS	2.5				

(Fig. 3). We also included the genus *Homo*, which was not included in Finarelli & Clyde's (2004) analysis; when included in other analyses, *Homo* falls within the polytomy of *Pan/Gorilla/Australopithecus* (Shoshani *et al.*, 1996; Strait *et al.*, 1997; Lieberman, 1999; Begun, 2001; Strait & Grine, 2004). This phylogeny is preferred over other morphological analyses for its large number of data (number of characters) and over molecular phylogenies for its inclusion of extinct taxa. Alternative topologies do exist. Strait & Grine (2004) and Collard & Wood (2000) produced hominoid phylogenies but these were based solely on cranio-dental characters. Young & MacLatchy (2003) ran several analyses using different combinations of characters, including Begun's, which resulted in numerous topologies. Finarelli & Clyde (2004) included a stratocladistic analysis in which they incorporated stratigraphic data (as a proxy for age) into the analysis. As in the case of Wagner's (1998) hyaenid tree, we do not use Finarelli & Clyde's stratocladistic hypothesis as an input phylogeny in order to avoid circularity. Both of these stratocladistic phylogenies will independently support or refute our biogeographical hypothesis, and are discussed further below.

Biogeographical analysis

Historical biogeographical relationships should be unique combinations of phenomena that affected multiple clades in the same way (general patterns) as well as those that are unique to a particular clade (clade-specific events) because of the complex and historically contingent nature of evolutionary history. Our ability to document these patterns is most obscured by the use of models and methods that oversimplify the analysis by invoking *a priori* assumptions or prohibitions. We can identify several essential elements of the analytical method required to study historical biogeography, which together form the basis for the new algorithm PACT [phylogenetic analysis for comparing trees (Wojcicki & Brooks, 2004, 2005)].

First, it is not permissible to remove or modify data. Wiley (1986a,b, 1988a,b) and Zandee & Roos (1987) formalized this as Assumption 0, which states that you must analyse all species and all hosts in each input phylogeny without modification, and that your final analysis must be logically consistent with all input data. When computer programs were developed that had the ability to handle missing data, Wiley (1986a) proposed using this coding for absences in a method he dubbed Brooks parsimony analysis (BPA), after Brooks' (1981) method. Assumption 0 does not imply that the input phylogenies are true or complete. It does imply that the method of analysis for biogeographical studies cannot be used to assess the accuracy of the phylogenies, as that would introduce an unacceptable degree of circularity into the process. Therefore, if one is dissatisfied with the results of a biogeographical analysis, and suspects that

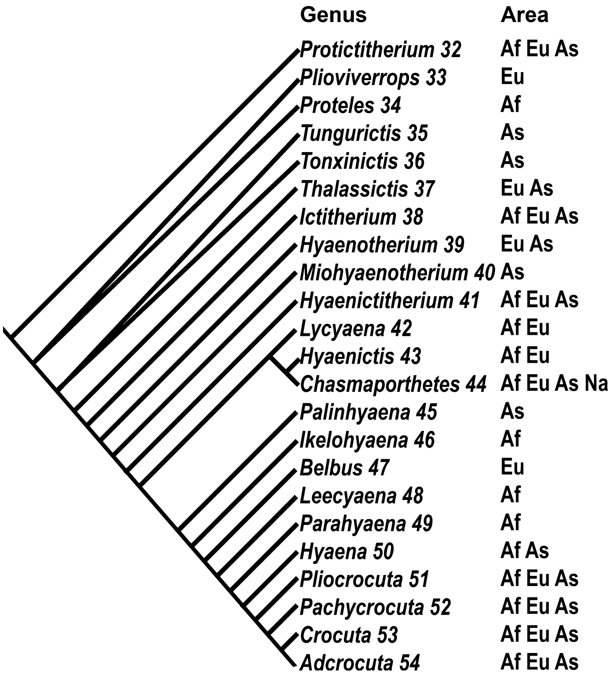

Figure 2 Hyaenid taxon and area cladogram (redrawn and modified from Werdelin & Solounias, 1991, 1996). (Range data are from Fortelius, 2005; Werdelin & Lewis, 2005.) Area(s) beside the genus name indicate the geographical range(s) in which the genus is found. AS: Asia, AF: Africa, EU: Europe, NA: North America, SA: South America.

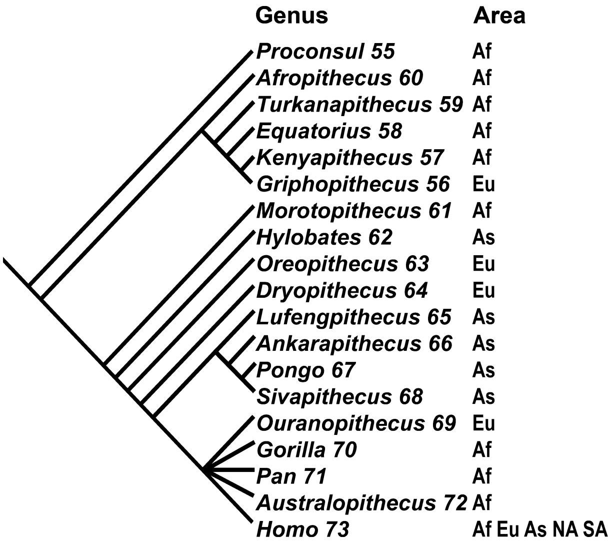

Figure 3 Hominoid taxon and area cladogram (redrawn and modified from Begun *et al.*, 1997; Finarelli & Clyde, 2004). (Range data are from Hartwig, 2002; Fortelius, 2005.) Area(s) beside the genus name indicate the geographical range(s) in which the genus is found. AS: Asia, AF: Africa, EU: Europe, NA: North America, SA: South America.

this is the result of a poor phylogenetic hypothesis or unsampled species, the solution is to obtain more data, improve the input phylogeny, and re-do the biogeography.

Second, area cladograms based on many clades inhabiting the same areas must include reticulated area relationships. If each area on this planet had a singular history with respect to all the species living in it, either there would be one species per area or one clade per area. Nowhere on Earth does this occur, so we must assume that reticulated area relationships have been common. Indeed, recent empirical studies using secondary BPA suggest that the majority of areas of endemism in published studies have reticulated histories (Brooks *et al.*, 2001; Green *et al.*, 2002; McLennan & Brooks, 2002; Spironello & Brooks, 2003; Bouchard *et al.*, 2004; Halas *et al.*, 2005). If we use a method of analysis that produces simple area cladograms (i.e. ones in which each area appears only once), Assumption 0 will be violated whenever an area has a reticulated history with respect to the species living in it. Assumption 0 can be satisfied in such cases by duplicating areas with reticulated histories. Therefore, a method of analysis for handling complexity requires a Duplication Rule, in which areas are listed for each event affecting them; this was first used by Brooks (1990) and formalized by Brooks *et al.* (2001) and Brooks & McLennan (2002).

Finally, if no possibilities, including area reticulations, are prohibited *a priori*, and if biogeographical patterns are combinations of unique and general phenomena, how are general patterns to be found? PACT employs Ockham's Razor as an epistemological corollary of the Duplication Rule – duplicate only enough to satisfy Assumption 0. Simplicity is used only to determine if there are general patterns, so this perspective is not a 'maximum dispersal' analogue of the maximum vicariance school. PACT searches for the maximum allowable general patterns as well as unique events and reticulated relationships. In this regard, it is most similar to secondary BPA (Brooks, 1990; Brooks & McLennan, 2002), but has been shown to be an improvement on that method (Wojcicki & Brooks, 2004, 2005). PACT produces a simple result when the data warrant it, but is capable of producing complex results when the data so demand.

Interpreting the area cladogram

Wiley (1981) was the first to suggest that various modes of initiating speciation could be studied phylogenetically, if biogeographical and population biological data were available, but only if two assumptions were made: first, there have been no extinctions in the clade; and second, the geographical context in which speciation was initiated has not been obscured by range expansion or contraction of the descendant species. It is likely that, for many groups, one or both assumptions are not justified. Even if a species is produced initially by vicariance, there is no guarantee that it will remain living happily within the confines of its ancestral distribution; the spectre of post-speciation dispersal or range contraction is always lurking in the background of any speciation study, particularly if the clades are old. Therefore, there is disagreement about the utility of Wiley's protocols in assessing the relative frequency of occurrence of particular modes of speciation (Lynch, 1989; Grady & LeGrande, 1992; Chesser & Zink, 1994). Green *et al.* (2002) suggested an alternative approach – one not relying on Wiley's assumptions. They suggested that historical biogeographical analysis of multiple, co-occurring clades could distinguish vicariant speciation, manifested in phylogenetic elements of each clade that conform to general biogeographical patterns, from other modes of speciation (and extinction), manifested as particular departures from those patterns.

Lieberman (2000, 2003a,b) proposed a protocol for distinguishing general nodes arising from vicariance from those arising from biotic expansion in area cladograms. For ambiguous cases, we assume vicariance as the default explanation.

Many cases of within-area speciation are likely to be episodes of vicariance (when a geographical barrier splits a formerly sympatric population) and peripatric speciation (also called peripheral isolates speciation, when a small number of individuals from one species splits off and becomes reproductively isolated) occurring on spatial scales smaller than those of the areas used in a particular analysis, or cases of peripatric speciation followed by post-speciation dispersal back into the ancestral area. Recognition of such cases requires additional information about geographical distributions within each area, probably resulting in further sub-division of the areas of endemism used, as well as information about habitat heterogeneity within each area and episodes of ecological diversification associated with particular speciation events (Brooks & McLennan, 2002).

RESULTS

PACT analysis of the taxon-area cladograms derived from the phylogenies of the three clades (Figs 1–3) produces the general area cladogram (GAC) in Fig. 4. The mapping of each taxon-area cladogram onto the GAC in Figs 5–7 provides visual demonstration that Assumption 0 has been satisfied. The GAC is complex, with many area reticulations and many widespread taxa, especially among the proboscideans. When combining input phylogenies, the default optimization in PACT is to match branches from the crown downwards, thereby mimicking DELTRAN optimization (or delaying transformations) in parsimony analysis.

With so many duplicated areas and widespread taxa, the potential for ambiguous placement of specific taxa would seem to be high. In some cases, the ambiguity is caused by the topology of the input cladogram. For example, the crown polytomy within Hominoidea (*Pan*, *Gorilla* and *Australopithecus*), since they are only found in Africa, could appear on any of the first six branches (from nodes A to F), after the placement of the widespread *Homo* at the tip because the order of their divergence is not resolved by the morphological phylogeny (Fig. 7). The ambiguous placements within the hyaenids are also related to the lack of resolution on the input cladogram: the two polytomies *Tungurictis*/*Tonxinictis* and *Protictitherium*/*Plioviverrops* are placed at nodes DD and FF respectively, but their exact placement will require further data.

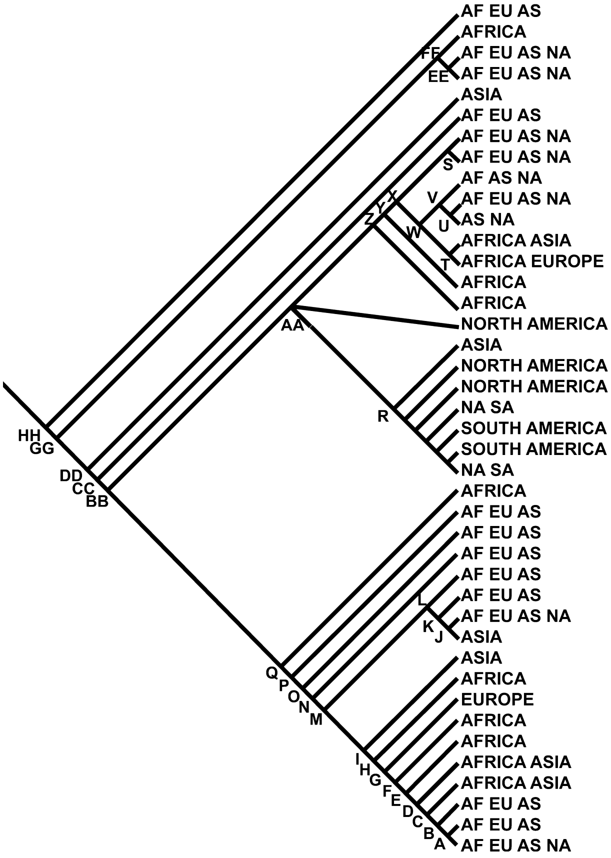

Figure 4 General area cladogram produced by PACT analysis of proboscidean, hyaenid and hominoid area cladograms (Figs 1–3). AS: Asia, AF: Africa, EU: Europe, NA: North America, SA: South America.

At the crown of the tree, the pectinate hyaenid input phylogeny forces 10 singular events that are specific to that clade and only partially replicated in the homoinoids and proboscids (Fig. 6). The four proboscidean species with African distributions (*Stegotetrabelodon*, *Stegodibelodon*, *Primelephas* and *Loxodonta*) could be placed on any of five nodes B to F. Similarly within the Proboscidea, the two widespread species *Stegolophodon* and *Stegodon* could appear on any of the three nodes J, K or L (Fig. 5).

The elephants undergo a radiation at node AA; the sheer number of species and their nearly universal widespread distribution result in two ambiguous placements of the other two clades within this general branch. The hyaenid species *Ictitherium* could occur on any of the branches with a shared distribution of Africa, Europe and Asia above node AA. Similarly, the early Miocene African hominoid *Equatorius* could be placed on any of the terminal branches above node X with Africa as part of the terminal area.

The first appearance of a hominoid (*Proconsul*) is ambiguous on the tree; the default PACT placement would be at node CC (Fig. 7), but it could appear earlier on a branch above node GG (all three branches show African elements), or at the first node (HH).

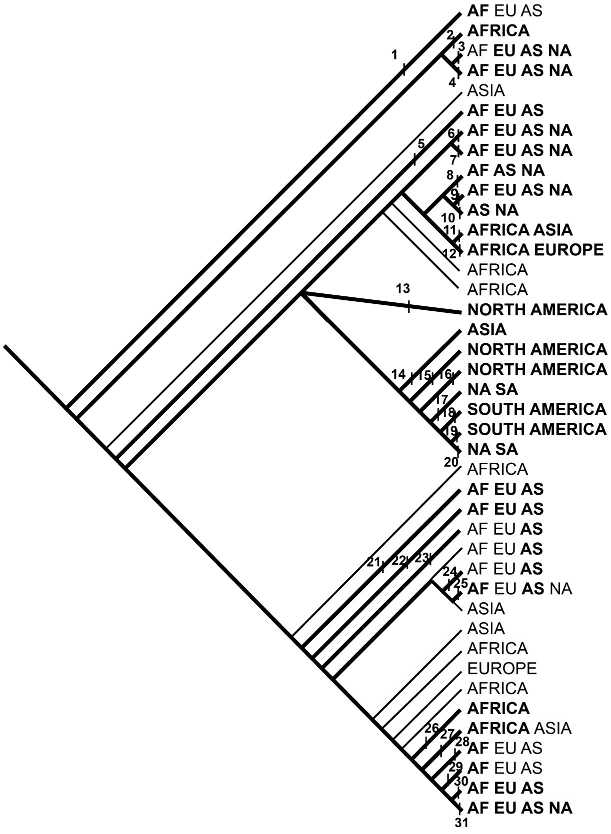

Figure 5 General area cladogram (GAC) with proboscidean area cladogram (Fig. 1) mapped on, demonstrating logical consistency with the input data. Thick lines are portions of the GAC in which proboscideans participated.

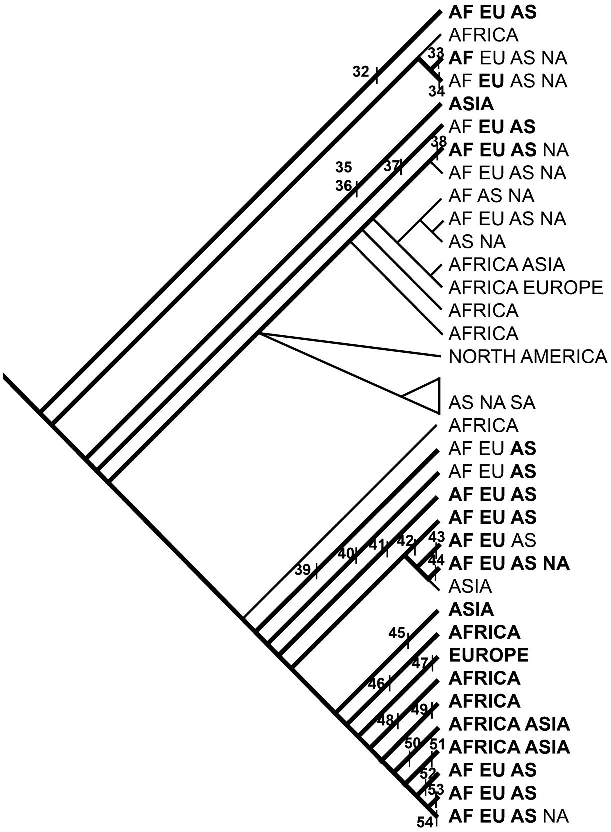

Figure 6 General area cladogram (GAC) with hyaenid area cladogram (Fig. 2) mapped on, demonstrating logical consistency with the input data. Thick lines are portions of the GAC in which hyaenids participated.

One way to assess the placement of these ambiguous taxa on the GAC is to look at first appearance dates (FADs); these dates provide a *minimum* age for each node (Table 1, Fig. 8). We recognize the limitations of the fossil record in terms of taphonomic bias and difficulties in dating nodes: that is, the phenomenon that recent taxa are almost always going to be better represented than more ancient ones (see Kidwell & Holland, 2002 for a review). Finarelli & Clyde (2004) demonstrated good congruence between stratigraphic (temporal) location and phylogenetic position in the Hominoidea, supporting the hypothesis that the fossil record is not as compromised as has been previously suggested.

The mapping of first appearances of taxa in the fossil record onto the GAC shows that the oldest taxa appear near the base and the youngest at the apical end (Table 1, Fig. 8). However, there is considerable variation, and in some cases the dates do not correlate at all. For example, at node O the hominoid representative, *Hylobates*, has no fossil record (thus a date of 0), the hyaenid *Hyaenotherium* first appears in the fossil record at 11 Ma, and the proboscidean *Tetralophodon* first appears at 12 Ma. These first appearance dates are minima for each node, and probably do not represent the actual ages of speciation events. There does appear to be generally good temporal correspondence between associated species from each clade and the minimum date of their appearance.

Having established the most robust mapping of the individual phylogenies on the GAC, we can optimize nodal inferences of areas as suggested by Lieberman (2003a) (Fig. 9). Of the 39 nodes on the GAC, six represent a radiation of gomphotheres into the Americas that was not duplicated in either the hyaenids or hominoids. For the purposes of this analysis, we collapse this clade and treat node R as a singular event within the Proboscidea. Of the other 34 nodes in the GAC, 17 (50%) are associated with concurrent events in all three clades (nodes A, B, C, J, K, L, M, N, O, P, S, X, Y, Z, AA, BB, CC), an additional nine (26%) are associated with events in two clades [nodes D, E, EE, FF, GG, HH (proboscideans and hyaenids), T, W (hominoids + proboscideans) and G (hominoids + hyaenids)], and eight (24%) are associated with an event involving a single clade [nodes R (which subsequently results in five more splitting events within the clade), U, V (proboscideans), F, H, I, DD (hyaenids) and Q (hominoids)]. The 26 nodes involving at least two of the three clades are designated the general nodes. Of these, nodes E, G, J, N, T and GG are vicariance (V) nodes; A, B, M, P, X, AA, BB, CC and FF are biotic expansion (BE) nodes; C, D, K, L, O, S, W, Y, Z and EE are widespread taxa (W) nodes; and the basal node

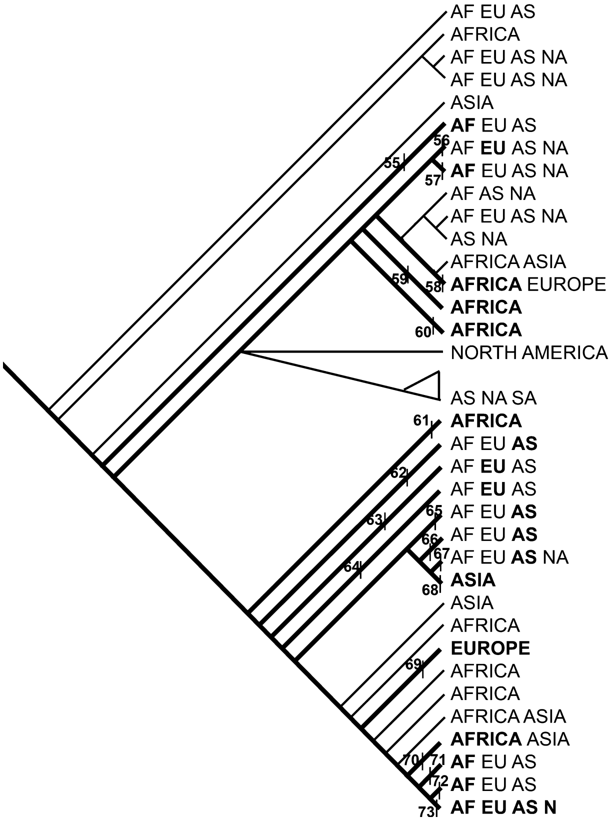

Figure 7 General area cladogram (GAC) with hominoid area cladogram (Fig. 3) mapped on, demonstrating logical consistency with the input data. Thick lines are portions of the GAC in which hominoids participated.

(HH) cannot be optimized without additional outgroups (Fig. 9).

In parallel with the caution with which we use first appearance dates, we recognize difficulties in delineating biologically relevant areas for biogeographical analysis. We have chosen to look at large-scale patterns of dispersal across continents, but realize that speciation probably takes place at much smaller scales. The resolution of this analysis is not as precise as that of those using smaller areas defined by existing geographical boundaries (Tougard, 2001; Halas *et al.*, 2005). This means that, among other things, the episodes we have designated as 'within-area speciation' do not necessarily imply frequent sympatric speciation events; rather, these probably indicate the limitations of the coarse spatial scaling used in this analysis. Future research could constructively be directed towards refining geographical ranges of these taxa and identifying past geological and/or geographical barriers to migration. Bearing these caveats in mind, the GAC supports the following interpretations illustrated in Figure 9.

At the basal-most node (HH), proboscideans are found only in Africa, while hyaenids occur in Africa, Europe and Asia. The hominoids do not have a representative at this node under PACT default settings (which place taxa higher up the tree), but the earliest hominoid, *Proconsul*, could be optimized to any of node HH, GG or the PACT default node CC. The ages of the taxa suggest a late Oligocene date for this node [the *Proconsul*-like hominoid *Kamoyapithecus* was dated to 24.2–27.5 Ma (Leakey *et al.*, 1995), and the proboscidean *Phiomia* was dated to 25 Ma (Shoshani & Tassy, 1996)].

Node GG is a vicariance node, where the hyaenids go from a widespread distribution to one event in Africa (node FF, *Proteles*) and one in Europe (node EE, *Plioviverrops*), and *Eozygodon* is found in Africa (ancestral area) (Fig. 9). At node FF, the proboscideans become widespread in an episode of biotic expansion and make their first foray into North America (*Zygolophodon* and *Mammut*). They undergo a within-area splitting event at node EE.

Node DD represents a minimum of one event in Asia by the two hyaenid genera *Tungurictis* and *Tongxinictis*; the input phylogeny (Werdelin & Solounias, 1996) does not resolve the relationship between the two, and without additional morphological data to resolve the relationship, the most parsimonious solution is a single case of peripatric speciation followed by within-area speciation. Node CC is a biotic expansion event involving all three clades. At this node, the proboscidean *Choerolophodon* disperses from Africa to become widespread across the old world. The hyaenids (*Thalassictis*) likewise speciate in the ancestral area of Asia and disperse into Europe. It is the first appearance of the hominoid clade, which occurs in Africa.

Node BB is a second biotic expansion node; this node represents the early Miocene African radiation of 'hominoids of archaic aspect' (Pilbeam, 1996; Finarelli & Clyde, 2004) and the Eurasian radiation of the gomphotheres and ambelodonts (Fig. 9). Along this branch, the hominoids speciate four times: three times in Africa (their ancestral area, at nodes X, Y, and Z) and then *Griphopithecus* expands the hominoid range to Europe at node S (Andrews & Tobien, 1977; Heizmann & Begun, 2001). At this node, *Griphopithecus* is associated with the hyaenid *Ictitherium*, which remains in its ancestral range (Europe and Asia) [and, depending on the affinities of several poorly known African specimens, may also be found in Africa (Werdelin & Turner, 1996)]. Along the branch from node BB, the proboscid clade undergoes an impressive radiation, in which it repeatedly disperses into all the continents. At node AA, the input cladogram is not resolved (Shoshani, 1996); the earliest gomphotheres are in Asia (*Sinomastodon*), and then a member of this lineage dispersed into North America and subsequently into South America in at least five divergence events. *Gnathabelodon* is a member of this polytomy; it may be on the lineage leading to the American radiation of gomphotheres, or along the ambelodont branch. Rather than postulating another independent dispersal event into North America, it is biogeographically most parsimonious for *Gnathobelodon* to have appeared along the American branch (node R). At nodes Y and Z along this branch, there are two single lineage-splitting events in the hominoids within Africa (*Turkanapithecus* and *Afropithecus*).

Node X represents a biotic expansion event shared by all three clades: the hominoids remain in Africa, the hyaenids

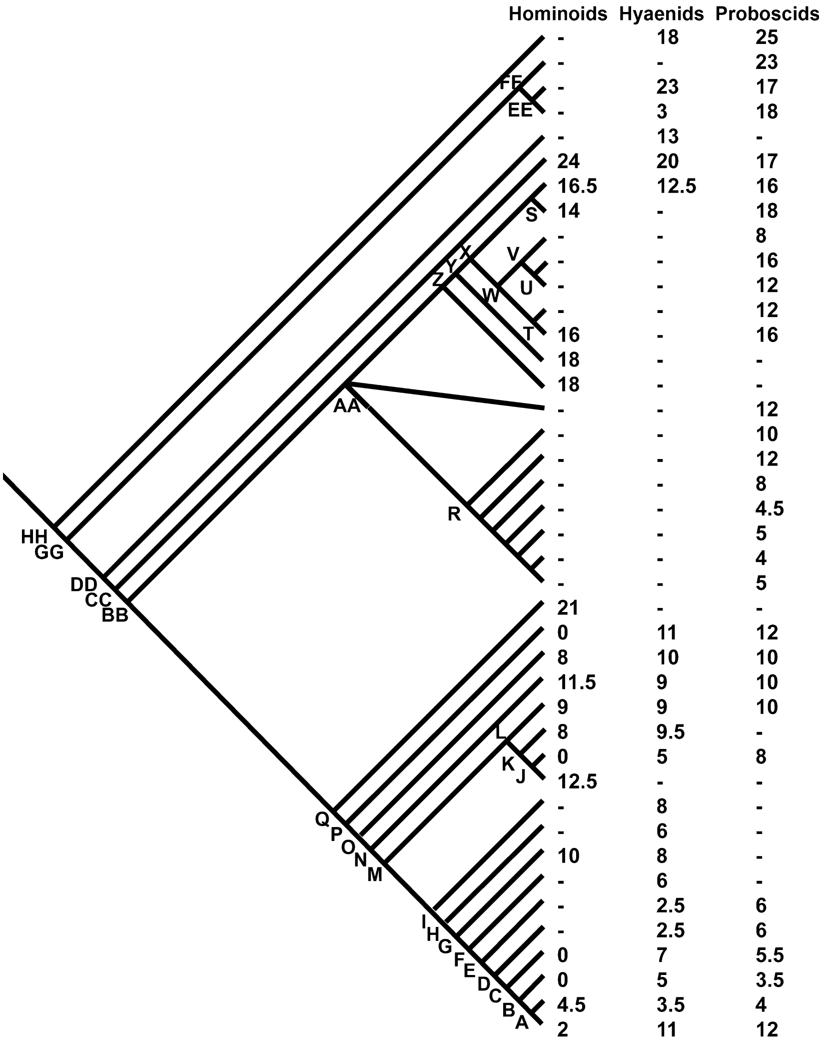

Figure 8 General area cladogram with dates of the earliest known appearance for each fossil taxon superimposed to the nearest 0.5 Myr (dashes reflect the absence of a terminal taxon in that particular clade).

remain in Europe and Asia, and the proboscids expand out repeatedly into all the continents (Fig. 9). Because the proboscids are widespread early, and remain in a widespread distribution, it is not possible to resolve the area of origin. The hominoids and hyaenids do not occur in the same area, and therefore their speciation events cannot be associated. These two clades may share events with the Proboscidea. Node T is a vicariant event for the homoinoids and proboscids: the elephants become restricted to Africa and Europe (*Archaeobelodon*) and Africa and Asia (*Protanancus*). Node W is a within-area event in the hominoids (Africa: *Equatorius*) and proboscids (widespread: *Ambelodon*, *Platybelodon*, *Serbelodon*, *Protanancus*, *Archaeobelodon*).

Node Q is a single within-area event in Africa by the hominoid *Morotopithecus* (Fig. 9). At node P, a biotic expansion event occurs: *Tetralophodon* becomes widespread, *Hyaenotherium* is found in Asia, and *Hylobates* penetrates into Asia from the ancestral area of Africa. This is the first occurrence out of Africa by the 'hominoids of modern aspect', and the hominoid area cladogram remains optimized to Asia from node Q up to node D. Node O is a within-area event: the proboscids (*Anancus*) remain widespread, the hyaenids (*Miohyaenotherium*) remain in Asia, and the hominoids (*Oreopithecus*) move from Asia into Europe. Node N is a vicariance node, with *Paratetralophodon* and the proboscids restricted to Asia, *Hyaenictitherium* becoming widespread from Asia into Europe and Africa, and the hominoid *Dryopithecus* remaining in Europe (within-area event).

Node M represents part of the biotic expansion begun at node N, and is associated with the origin and isolation of ancestral members of all three clades in Asia (Fig. 9). The proboscids appear at two nodes on this branch and remain in the ancestral area of Asia (node K, *Stegolophodon*), and then there is an episode of post-speciation dispersal after divergence in Asia (node J, *Stegodon*). The hyaenids remain widespread (node L, *Lycaena*; node K, *Hyaenictis*) and then expand out into North America (node J, *Chasmaporthetes*). The hominoids enter Asia from their ancestral area of Europe, and speciate within that continent in three events at this node (*Lufengpithecus*, *Ankarapithecus*, *Pongo* and *Sivapithecus*). There is a second biotic expansion event at node L.

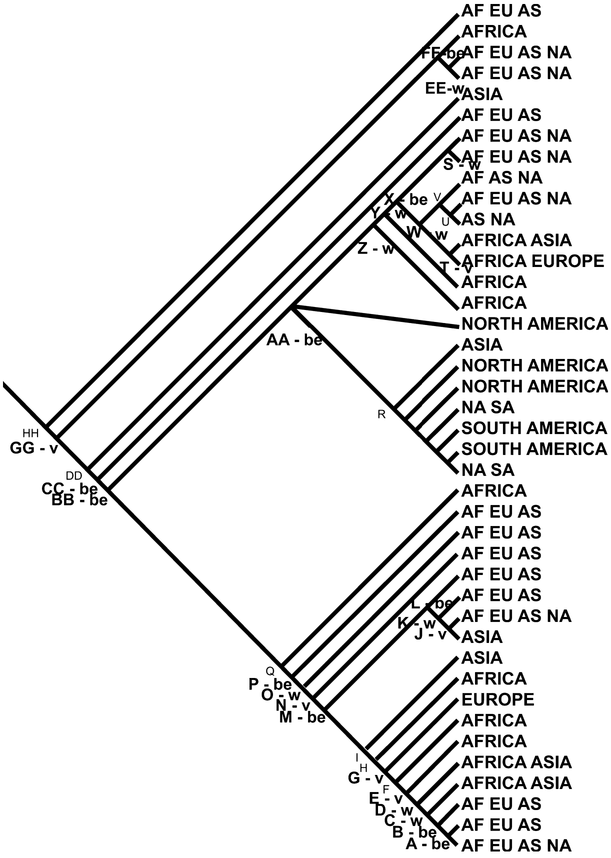

Figure 9 General area cladogram, with general nodes resulting from vicariance (V), biotic expansion (BE), and those affecting multiple clades in widespread areas (W) labelled. The determination of V vs. BE follows the protocol of Lieberman (2000, 2003a,b). All other nodes reflect unique events affecting only a single clade. See text for details.

Nodes I and H are unique splitting events involving hyaenids interpreted as peripatric speciation in Asia (*Palinhyaena*) and Africa (*Ikelohyaena*) during the more general biotic expansion out of Asia. There is a vicariance event in Europe involving *Ouranopithecus* and the hyaenid *Belbus* (node G).

At node F, the general pattern shows optimization to Africa; this is part of the vicariant event from node G that sees members of all three clades change in distribution from a series of Asian origins by its members to a series of speciation events occurring in Africa. *Leecyaena* occurs at node F in a singular event. Node E is another vicariance event in Africa, in which two of the three clades participate (the proboscid *Stegotetrabelodon*, and hyaenid *Parahyaena*). There is another episode of within-area speciation in Africa (node D) involving *Stegodibelodon* and *Hyaena* (which disperses post-speciation into Asia). Node C is more within-area speciation, this time with the participation of the hominoids (*Gorilla*) as well as the African *Primelephas* and the widespread hyaenid *Pliocrocuta*. At node B, there is an African divergence of *Loxodonta* and *Pan*, with a widespread hyaenid (*Pachycrocuta*). This node signals the beginning of another episode of biotic expansion out of Africa. At node A, all three clades disperse out of Africa again to colonize all the continents within the study. *Elephas* and *Crocuta* are found in Africa, Europe and Asia, while *Australopithecus* remains in Africa. The final event produces the three widespread genera *Mammuthus* (which disperses into North America), *Adcrocuta*, and *Homo* (which also disperses into Eurasia and North and South America).

DISCUSSION

Hominoids, hyaenids, and proboscideans have been associated with each other at least since the early Miocene, as evidenced by their shared presence at various fossil localities. The results, however, do not conform to a simple vicariance scenario. Rather, they exhibit the alternating episodes of vicariance and biotic expansion embodied in the 'taxon pulse hypothesis' (Erwin, 1979, 1981), summarized in Fig. 10.

Initially, the three clades are all found in Africa (proboscideans and hyaenids at node HH, and hominoids at node CC), but this does not imply an African origin for each of the three clades individually. This African optimization is a result of the arbitrary cut-off of 25 Ma that we used in the analysis, and the inclusion of additional, older outgroups would clarify the geographical ranges and origins of the earliest taxa. At node GG there is a vicariance event involving the hyaenids and proboscids; these two clades later undergo further dispersal and speciation together (nodes EE and FF). Nodes CC and BB probably reflect two parts of the same biotic expansion event involving dispersal from Africa and subsequent speciation (Out of Africa 1 – OOAf^1). Between nodes DD and Q in the middle of the general area cladogram, there are four general biotic expansion nodes involving taxa expanding their ranges out of Africa and diversifying in Eurasia.

Node P is a biotic expansion event out of Africa that begins the next sequence of speciation events (Fig. 10). The GAC is optimized to Asia at this point, suggesting an Asian origin for most taxa. Node N indicates a vicariant event isolating Asia. This isolation event is followed by two parallel episodes of biotic expansion from Asia (OOAs^1 and OOAs^2), beginning at node M.

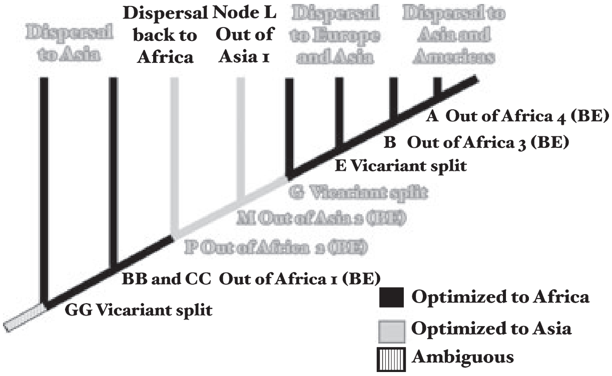

Figure 10 Summary of conclusions: general area cladogram with major episodes of taxon pulse diversification highlighted on the nodes at which they occur. BE: biotic expansion.

At node G, there is another vicariant event, where most taxa go extinct in Eurasia and are restricted to Africa. At node E there is vicariant isolation in Africa followed by within-area speciation (nodes C and D), and then two more episodes of biotic expansion out of Africa (nodes B and A) (OOAf^2, OOAf^3) (Fig. 10).

Within this general pattern of taxon pulse-driven biotic evolution, each group exhibits clade-specific histories of speciation and extinction.

Proboscidea

The proboscidean clade is characterized by a large number of widespread taxa, which presumably originated in a restricted area and then dispersed throughout contiguous continental landmasses, making it difficult to determine areas of origin. Their widespread distributions are probably related to their large body size: elephants require a large geographical range for resources, and they are capable of long-distance travel. In addition, some elephant species (mammoths and mastodonts) were clearly well adapted for living in cold climates, which indicates a certain degree of environmental flexibility. It appears that the proboscideans underwent a burst of diversification and speciation relatively early in the Miocene (node BB) (see also Fig. 5). The clade has at least two major episodes of speciation resulting in at least two complex arrays of closely related taxa, the ambelodonts and gomphotheres at node AA. These taxa first appear in the early Miocene and their age spans through the end of the Miocene into the Pleistocene (Fig. 8).

There is an earlier, smaller radiation of the *Eozygodon/Zygolophodon/Mammut* group at node GG. This analysis supports Saegusa's (1996) hypothesis of a south-east Asian centre of radiation for the Stegodontidae during the mid-late Miocene (nodes M, N, O, P). There is a third range expansion in the proboscids (mirrored in the hyaenids and hominoids) in recent times (node A). The earliest record of *Mammuthus* is in the mid-Miocene, which produces a very long ghost lineage; this is similar to the hyaenid representative at node A, *Adcrocuta*, which also originates in the mid-late Miocene, yet appears at the crown of the tree. In this case, we can use temporal as well as biogeographical data to constrain the fit of the taxa to the GAC.

Of the approximately 60 species of proboscidean considered in this study, there are only two living species of African elephant (*Loxodonta africana* and *L. cyclotis*) (Roca *et al.*, 2005) and one living species of Asian elephant (*Elephas maximus*) (Kalb *et al.*, 1996a,b).

Hyaenidae

The hyaenid input cladogram was highly pectinate (Figs 2 and 6), which results in few splitting events within the clade that produce more than a single species. This clade shows the same general pattern as the proboscids [origin widespread, possibly African (Werdelin & Turner, 1996)], then a primarily Eurasian distribution in the middle of the GAC, with one genus (*Chasmaporthetes*) crossing the Bering Strait to North America, and then a more recent contraction into Africa and then back into Eurasia.

Wagner (1998) constructed maximum likelihood trees that incorporate stratigraphic information, attempting to minimize both morphological and temporal instances of homoplasy. These trees differ from Werdelin & Solounias' (1991, 1996) topologies – they are less pectinate, and find two distinct clades of hyaenids. The maximum likelihood trees find a Eurasian origin of the clade (with basal members *Plioviverrops*, *Tungurictis* and *Ictitherium*), then a clade of primarily Eurasian species, with a switch to widespread and African-distributed species at the crown of the cladogram. This is a general pattern similar to the events documented on the GAC using the maximum parsimony phylogenies. Wagner's trees both place *Adcrocuta* more basally on the tree, probably as a result of its early appearance date (11 Ma). As we have shown, however, the proboscids show the same pattern, with *Mammut* at the crown of the tree but appearing very early in the fossil record. This may be a case where an early member of a clade persists over a long period of time, and, in both these cases, becomes distributed over a wide area. This pattern would not have been visible without a comparison of taxa from disparate clades.

Hyaenids are responsible for four of the eight clade-specific events on the GAC. This may suggest a more constant rate of species formation for hyaenids than for the other two clades. Like the proboscideans, almost all hyaenids are extinct: of the 62 species considered, only four are extant (Werdelin *et al.*, 1994; Werdelin & Turner, 1996).

Hominoidea

Using the PACT default, the hominoids originate in Africa (*Proconsul* at node CC). The temporal data (proconsulids first appear *c.* 24 Ma) support an earlier origin of this taxon – possibly at node GG with the African *Eozygodon* (*c.* 23 Ma). Then there is a small clade-specific radiation within Africa at node BB (*Kenyapithecus*, *Equatorius*, *Turkanapithecus and Afropithecus*); not until the origin of *Griphopithecus* (16.5 Ma) at the tip of this branch do the hominoids disperse from Africa (Fig. 7). At the general biotic expansion node P, the hominoids have left Africa and are no longer found there; the members of the clade undergo at least eight splitting events in Eurasia, and form a clade of sivapithecines, including the living *Pongo*.

Following the appearance of *Ouranopithecus* at node G, there was a vicariant event in which hominoids returned to Africa and diversified (*Gorilla*, *Pan*, the 'australopiths'). Subsequent to that, *Homo* expanded out of Africa during the Pleistocene, setting the stage for the evolution of modern humans.

Finarelli & Clyde (2004) provided further support for the completeness of the hominoid fossil record. They observed a 'better-than-average match' (2004, p. 634) between the first appearance dates of hominoids and the topology of the most parsimonious trees, which suggests that the ghost lineages (or missing fossil data) are not long. Like Wagner (1998), they recovered a stratocladistic tree (although based on parsimony rather than maximum likelihood). Although this tree differs from their most parsimonious morphological tree (figured here in Fig. 3), it reflects the same general pattern as recovered in our GAC. The earliest hominoids are African in distribution (*Proconsul*, *Morotopithecus*, *Turkanapithecus*, *Afropithecus* and *Equatorius*). With the appearance of *Griphopithecus*, the optimization of the area cladogram changes to Europe and Asia, then back into Africa at the node below *Australopithecus*. Again, the details differ with respect to the nodes leading to particular species, but the general pattern is supported, and reveals more detailed information than can be recovered by morphological, stratocladistic or area cladograms alone.

From the late Miocene to present, there are numerous hominine genera known (including *Orrorin*, *Sahelanthropus*, *Dryopithecus*, *Kenyanthropus*, *Ardipithecus*, *Australopithecus*, *Praeanthropus*, *Paranthropus*, *Homo*, *Samburupithecus*, *Udabnopithecus*), and within those genera a constantly increasing number of species are being discovered and/or recognized (Wood & Collard, 1999; Lieberman, 2001; Ward & Duren, 2002; White, 2002; Cameron, 2003). During the past 2 Myr alone, as many as nine species may have evolved in the genus *Homo*, all but one of which have gone extinct (*H. habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. antecessor*, *H. neanderthalensis*, *H. floresiensis*?, *H. sapiens*) (Schoetensack, 1908; Robinson, 1965; Wood, 1992; Bermúdez de Castro *et al.*, 1997; Wood & Collard, 1999; Dunsworth & Walker, 2002; Brown *et al.*, 2004; Strait & Grine, 2004). If all those nominal species were evolutionarily distinct, speciation rates within the hominin clade accelerated significantly during the past 2 Myr. We recognize the improbability that these are all distinct species; with more data and study, it is likely that some of these taxa will be consolidated. This may or may not make a significant difference in the abundance of fossil species. There is also the possibility that the increased diversity is a taphonomic result of better preservation of more recent fauna. However, we would expect this to be paralleled in the proboscideans and the hyaenids, which it is not. Thus, unless the apparent increase in variability within taxa sampled is a result of taphonomic or nomenclatural bias, our analysis supports the hypothesis that hominin diversification experienced a clade-specific acceleration in the past 5 Myr.

CONCLUSIONS

Studies focussing solely on hominoids have suggested an Asian or Eurasian origin of the African ape–human clade (Begun, 1997; Stewart & Disotell, 1998; Begun, 2001). This study corroborates those results, and situates hominoid diversification within the complex history of diversification and extinction of large land vertebrates during the Miocene epoch. The dispersal of *Homo* out of Africa in the Pliocene was not a unique event in human evolution, but just another episode in the taxon pulse diversification of Old World biotas.

Hominoids, proboscideans, and hyaenids were associated in Africa at least as early as the early Miocene epoch. Vicariant isolation in Africa and Asia during the early Miocene was followed by biotic expansion out of Africa. Vicariant isolation in Asia in the middle Miocene led to two major episodes of biotic expansion out of Asia, which resulted in taxa colonizing the Americas, Europe and Africa. In the late Miocene and Pliocene, two additional episodes of vicariant isolation in Africa were each followed by biotic expansion out of Africa. Part of this scenario has been suggested previously for hominoid evolution (Vrba, 1992; Pickford & Morales, 1994; Agustí *et al.*, 2001) and has been attributed to climatic change. Europe experienced a warming trend during the middle Miocene, which may have made it more hospitable for hominoid habitation, and at the end of the Miocene a cooling trend caused the localized extinction of hominoids, and re-entry into Africa (Cerling *et al.*, 1997). Our study suggests that proboscideans and hyaenids may have responded in the same general manner to these events.

PACT adds two critical elements to studies of historical biogeography. First, it permits complex patterns to be found in complex data. Second, and following from the first, PACT facilitates the integration of fossil and recent taxa. If we look only at the geographical distributions and relationships of extant hominoids and their sister group, the cercopithecoids, the ancestral distribution would be interpreted as African, with movement to, and then diversification within, Asia (hylobatids and orangutans), followed by a return to Africa and additional diversification (gorillas, chimps, humans), with additional dispersal out of Africa (humans). Co-evolutionary analysis of some hominoid parasites, using PACT (Brooks & Ferrao, 2005), produced the same biogeographical patterns. In this study, we have shown that clades composed wholly or mostly of extinct taxa provide added depth and breadth to biogeographical analyses based only on extant taxa (Novacek, 1992), identifying additional general episodes and clade-specific events involving clades with which hominoids were associated ecologically. Finally, this study adds palaeontological support to other recent studies that suggest that the major driver of biotic diversification has been taxon pulses rather than simple vicariance (Spironello & Brooks, 2003; Bouchard *et al.*, 2004; Halas *et al.*, 2005).

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